FROM METAZOAN TO PROTIST VIA COMPETITION AMONG CELL LINEAGES

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ABSTRACT: Competition among genetically variant cell lineages has recently resulted in the evolutionary transition from metazoan to protist. Some of the new protists have extended their geographic range to other continents and continue to compete with other protists that originated in the same way. The change in grade of organization from multicellular to unicellular and the origin of new species has occurred in a saltatory step that is brief on an ecological time scale and instantaneous in geologic time. These evolutionary changes follow more than 5×10^8 years of stasis.

Somatic Cell Selection

In so far as multicellular animals are composed of genetically identical cells, one would expect a high degree of cooperation among the cells comprising a multicellular animal. When all cells of a multicellular organism are of the same genotype, selection among cell lineages should not occur. Selfish cell lineages are unexpected; cooperation among cell lineages is expected, and there is no conflict between selection among individuals and selection among their component cells (Raff, 1988; Van Valen, 1988). Buss (1987) has advanced an intriguing alternative hypothesis: because genetic variants arise within multicellular organisms, genetically distinct cell lineages may compete with each other for resources and for inclusion in the germ line.

For hypotheses about evolution and adaptation, it is often not a question of whether the hypothesis is false but whether it is broadly or narrowly applicable to organisms. Here the hypothesis is that within multicellular organisms selection can favor genetically variant cell lineages that gain more entrance to the germ line. Discussions of Buss's (1987) book tend to emphasize difficulties in this hypothesis (Raff, 1988; Van Valen, 1988; Bell, 1989). Here I note a confirming case, in which protists have evolved from multicellular animals. To appreciate this case, one must first consider the limits on selection among cell lineages when the cells remain parts of metazoans.

Persistence of Genetically Variant Cell Lineages in Metazoans

Genes that increase cells' access to the germ line encounter a problem when the cells have produced the next generation (Raff, 1988; Van Valen, 1988; Bell, 1989; Wolpert, 1990). A multicellular animal composed entirely of such cells will at best have no selective advantage relative to the original genotype and is likely to be at a disadvantage because of impaired somatic functions. Thus in the majority of metazoans, such genetically variant cell lineages have poor prospects beyond the generation in which they arise.

Competitively dominant metazoan cell lineages have more potential in animals that commonly fuse to form chimaeric individuals. In these cases, a cell type that is superior in gaining access to the germ line could persist indefinitely. Competitive cell lineages could be propagated within animals composed largely of cooperative cell lineages; survival of the competitive cell lineages does not

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depend on the fitness of an organism composed entirely of such cells. Buss's (1982) "somatic cell parasites" among slime molds may provide an example, and examples might be sought among colonial metazoans that form chimaeric individuals by fusion (Grosberg and Quinn, 1986; Jackson, 1986). Such cell lineages would appear to be dependent on a host of the same species, and their success would be frequency dependent (Buss, 1982).

Transformation of Genetically Variant Cell Lineages into Protists

Another possibility is that a genetically divergent cell lineage of a multicellular animal could become in effect unicellular protists. In such a case all the unicellular descendants are in the germ line. (The term protist applies to a grade of organization rather than a monophyletic group. It is therefore acceptable to lump convergently unicellular eukaryotes into the protists.) A familiar example of competition among cell lineages with deleterious effects for the multicellular organism is the multiplication of cancerous cells. If cancerous cells should survive as protists, the evolutionary route would involve differential proliferation of cell lineages both at the origin of the protist and in its continuing survival. Their persistence would not depend on frequent formation of chimaeric multicellular organisms. In these respects, protists derived from carcinomas would have greater evolutionary potential than somatic cell parasites. Are such events known?

Buss (1987) mentions dissolution into unicellular protists as a potential developmental problem during the early stages in the evolution of multicellular organisms. Though such an event may still occur in organisms such as the alga Volvox (Bell, 1989), this evolutionary route is improbable for the Metazoa during most of their history because cells formerly adapted for life in a multicellular animal would be poorly equipped as protists in comparison to cell lineages selected for performance as unicellular organisms through many preceding generations. Circumstances have recently changed, however, and in the last few decades there have been some extraordinarily successful transitions from metazoan to protist. These are the cells that have been brought into tissue cultures for biomedical research. Among the most successful, in longevity and range extension, have been cancerous cells. It is now possible for a metazoan cell lineage to kill its sister cell lineages and survive indefinitely.

Some of these cell lineages are strikingly successful as unicellular organisms. Some have invaded and displaced other cell lineages in tissue culture despite the efforts of biomedical researchers to keep cell lineages of different origin separate (Gartler, 1968; Nelson-Rees et al., 1981). Gold's (1986) book on the spread of HeLa cells can be read as an account of the evolutionary ecology of these new protists. HeLa cells (from a carcinoma of a human cervix) have been notably aggressive in invading tissue cultures and have extended their biogeographic range from North America across oceans to other continents. These cells and others like them continue to compete with other cells, to extend their geographic ranges, and to evolve after leaving the metazoan individual of their origin.

Though the possibility has existed for less than 10^{-7} of Phanerozoic time, competition among genetically variant cell lineages of multicellular animals is currently a route by which protists can originate from metazoans. Biomedical research laboratories that use tissue cultures have made the metazoan to protist transition a common event. After more than 5×10^8 years of stasis as metazoans, a genetic change can produce a cell lineage of effective protists in one saltatory macroevolutionary step. The time required for this transition is short on an

ecological time scale and instantaneous on a geological time scale. No example from the fossil record has documented such an abruptly punctuated equillibrium.

For a transformed cell lineage from a carcinoma to become a successful protist, it must establish a symbiosis with human biomedical researchers. For those interested in levels of selection, both competition among cell lineages and cultural evolution are elements in the success of these new protists. The memes (Dawkins, 1976) of the biomedical research community are interacting with genetically variant cell lineages in the origination and continued evolution of these "selfish cell lineages."

This evolutionary route has resulted from cultural developments in a single species of primate, but it is an evolutionary route that can produce protists from a great variety of metazoan species. These cell lineages are asexual and thus meet the biological definition of a new species: they do not interbreed with their sister metazoan species. Though asexual, they do have the potential to gain new genetic material by cell fusion (Barski et al., 1961) and through viral infection. Like other domesticated species, cancerous cells of non-human origin have the potential to spread beyond the geographic range of their metazoan sister lineages and outlive them.

It is beyond dispute that selection among somatic cell lineages has led to a change in grade of organization and that the new organisms persist, evolve, and expand their geographic range. However, I have encountered several biologists who dismiss the examples from tissue culture because they involve an artificial rather than a natural system. I do not see the force of this argument. Even if one considers biomedical researchers engaged in tissue culture to be artificial or unnatural, they could still be part of an important evolutionary process. These days, much of what happens to populations of organisms involves human intervention. Another distinction is between common and rare circumstances. Does rarity make an evolutionary event uninteresting? Not necessarily; events at the Cretaceous-Tertiary boundary were unusual, yet many evolutionary biologists find them interesting. The consequences of an evolutionary event provide other criteria for its importance or triviality. Developmental and other functional consequences of successful lineages of cancerous cells are large, but the ecological consequences remain slight. They are not yet having much impact on other organisms or on biogeochemical fluxes. If the ecological criterion for interest is widely accepted, then this example can be dismissed. If relevance to general theoretical issues is the criterion for interest, then the example deserves attention.

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References

Barski, G., S. Sorieul, and F. Cornefert. 1961. 'Hybrid' type cells in combined cultures of two different mammalian cell strains. J. Natl Cancer Inst. 26:1269-1291.

Bell, G. 1989. Darwin and biology. J. Heredity 80:417-421.

Buss, L. W. 1982. Somatic cell parasitism and the evolution of somatic tissue compatibility. Proc. Natl Acad. Sci. U.S.A. 79:5337-5341.

Buss, L. W. 1987. The Evolution of Individuality. Princeton University Press, Princeton. 201 pp.

Dawkins, R. 1976. The Selfish Gene. Oxford University Press, Oxford.
Gartler, S. M. 1968. Apparent HeLa cell contamination of human heteroploid cell lines. Nature 217:750-751.
Gold, M. 1986. A Conspiracy of Cells. State University of New York Press, Albany. 170 pp.
Grosberg, R. K., and J. F. Quinn. 1986. The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. Nature 322:456-459.
Jackson, J. B. C. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. Bull. Mar. Sci. 39:588-606.
Nelson-Rees, W. A., D. W. Daniels, and R. R. Flandermeyer. 1981. Cross-contamination of cells in culture. Science 212:446-452.
Raff, R. A. 1988. The selfish cell lineage. Cell 54:445-446.
Van Valen, L. M. 1988. Is somatic selection and evolutionary force? Evolutionary Theory 8:163-167.
Wolpert, L. 1990. The evolution of development. Biol. J. Linn. Soc. 39:109-124.